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TWO NEW DISCODORID NUDIBRANCHS FROM THE
WESTERN PACIFIC WITH A REDESCRIPTION
OF *DORIS LUTEOLA* KELAART, 1858

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Two new species of discodorid cryptobranch dorid nudibranchs are described from the tropical Indo-Pacific. *Hoplodoris estreyado* is found from several localities in the western and central Pacific: Vietnam, Western Australia, Indonesia, Philippines and the Marshall Islands. It is the only member of the genus in which all of the radular teeth are denticulate. *Taringa halgerda* is known from Papua New Guinea, the Philippine Islands and Indonesia. It is similar in appearance to *T. luteola*, but differs in its coloration and tubercles and aspects of its internal anatomy. *Taringa luteola* (Kelaart, 1858) is redescribed and its systematic placement is discussed.

Placement of the two species described here is regarded as tentative. Neither *Hoplodoris estreyado*, *Taringa luteola* nor *Taringa halgerda* are placed with certainty in the genera where they are here assigned. They possess characteristics that are divergent from other described members of the genera *Hoplodoris* and *Taringa*. A major review and revision of dorid genera is required. Phylogenetic analysis would clarify the relationships between and within taxa and would determine which taxa represent monophyletic groups. Systematic revisions would then be made to reflect these monophyletic units.

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The tropical Indo-Pacific is rich in its diversity of opisthobranch gastropods (Gosliner 1992; Ghiselin 1992; Gosliner and Draheim 1996). Annual field collections in the Philippine Islands over the past several years have yielded specimens of numerous new species of opisthobranchs. Several of these have been recently described (Gosliner and Behrens 1997, 1998) or their descriptions are presently in press. This paper describes two new species of cryptobranch dorid nudibranchs and compares them to other species that are similar in appearance.

The status of the systematics of the doridacean nudibranchs, especially the Cryptobranchia, is in need of much revision. The separation of genera and their organization into families has been undertaken on an ad hoc basis, without employing phylogenetic methods. Many presently recognized genera are based on what are likely plesiomorphic characteristics and represent paraphyletic taxa. Problems associated with taxonomic allocation of species are illustrated by the difficulties presently encountered in placing the two species described here into well-circumscribed genera.

SPECIES DESCRIPTIONS

Family DISCODORIDIDAE

***Hoplodoris estrelyado* sp. nov.**
(Figs. 1A, 2, 3)

Hoplodoris nodulosa (Angas): Debelius, 1996:253, two bottom photos; not (Angas, 1864).

Discodoris sp. Gosliner, Behrens and Williams, 1996:159, fig. 558.

TYPE MATERIAL. — Holotype: CASIZ 088114, one specimen, Twin Rocks, SW Calumpan Peninsula, Batangas Province, Luzon, Philippine Islands, 18 m depth, 4 March 1993, T. M. Gosliner. Paratypes: CASIZ 085950, one specimen, dissected, Bus Stop Reef, Balayan Bay, Batangas Province, Luzon, Philippine Islands, 8 m depth, 24 March 1993, T. M. Gosliner. CASIZ 105664, three specimens, Hamilo Bay – The Head, Batangas Province, Luzon, Philippine Islands, 13 m depth, 4 March 1995, T. M. Gosliner. CASIZ 088113, one specimen, Devil's Point, Maricaban Island, Batangas Province, Luzon, Philippine Islands, 13 m depth, 23 May 1993, M. D. Miller. CASIZ 110459, one specimen, Cathedral Rock, Balayan Bay, Batangas Province, Luzon, Philippine Islands, 13 m depth, 23 May 1993, M. D. Miller.

ETYMOLOGY. — The trivial name *estrelyado* is the Tagalog word for "sunny side up" which is derived from the Spanish word "estrella," for star, indicating the eggs are formed into starlike patterns with the yolk shining upwards. This applies to the unique color pattern on the notal surface, giving the appearance of fried eggs, served sunny-side up.

DISTRIBUTION. — Thus far, this species is known from Vietnam and Western Australia (Debelius 1996), Indonesia, the Philippine Islands (present study), and the Marshall Islands.

NATURAL HISTORY. — *Hoplodoris estrelyado* is found on the outer edges of rock walls and reef fronts in 5–30 m of water.

EXTERNAL MORPHOLOGY. — The living animals (Fig. 1A) are 15–40 mm in length. The body

is oval and flat, the notal surface covered with large tapering tubercles (Fig. 2A), which lack spicules that project from the tubercles. The coloration of the living animals is complex and strikingly unique. The ground color of the notal surface is translucent tan with dark brown and white specks. An oval pattern of tubercles resembling fried eggs, a white patch with yellow center, surrounds a medial group of dark brown tubercles. The size of the white, egg-like ring becomes smaller on the tubercles nearer the margin. The tubercles forming the 6–8 largest fried-egg patterns are each encircled by 8–10 smaller white tubercles. A few tan colored tubercles are dispersed about the notal surface, and are particularly abundant near the center of the notum. The underside of the foot and mantle are speckled with dark brown. The anterior margin of the foot is bilabiate and notched. On either side of the head is a long, digitiform tentacle which also is covered with brown speckles. Six tripinnate branches form the branchial plume, which is tan with dark brown and white specks. The anus is situated within the gill circle. The perfoliate rhinophores bear about 13–19 lamellae and are dark reddish brown with white specks.

BUCCAL ARMATURE. — The buccal mass is large and muscular. At the anterior end of the muscular portion of the buccal mass is the thin, chitinous labial cuticle. It contains a pair of thickened triangular regions anteriorly that bear numerous irregularly tipped rodlets (Fig. 3A). The radular formula in one specimen is $26 \times 65.0.65$. The innermost lateral teeth (Fig 3B) are hamate with two minute, irregular denticles along the outer edge of the tooth. The radular teeth from the middle of the half-row (Fig. 3C) have a far more elongate cusp with up to 11 minute denticles on the outer margin. The teeth from the outer margin of the radula (Fig. 3D) have shorter, thicker cusps with 6–11 denticles along the outer margin.

REPRODUCTIVE SYSTEM. — The reproductive system is triaulic (Fig. 2B). The ampulla is thick and tubular, narrowing somewhat before bifur-

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FIGURE 1. Living animals. A. *Hoplodoris estrelyado* sp. nov., specimen from Batangas Province, Philippine Islands, photograph by T. M. Gosliner. B. *Taringa lutcola* Kelaart, 1858, Msimbati, Tanzania, photograph by T. M. Gosliner. C. *Taringa halgerda* sp. nov., specimen from Bus Stop Reef, Batangas Province, Philippine Islands, photograph by T. M. Gosliner.



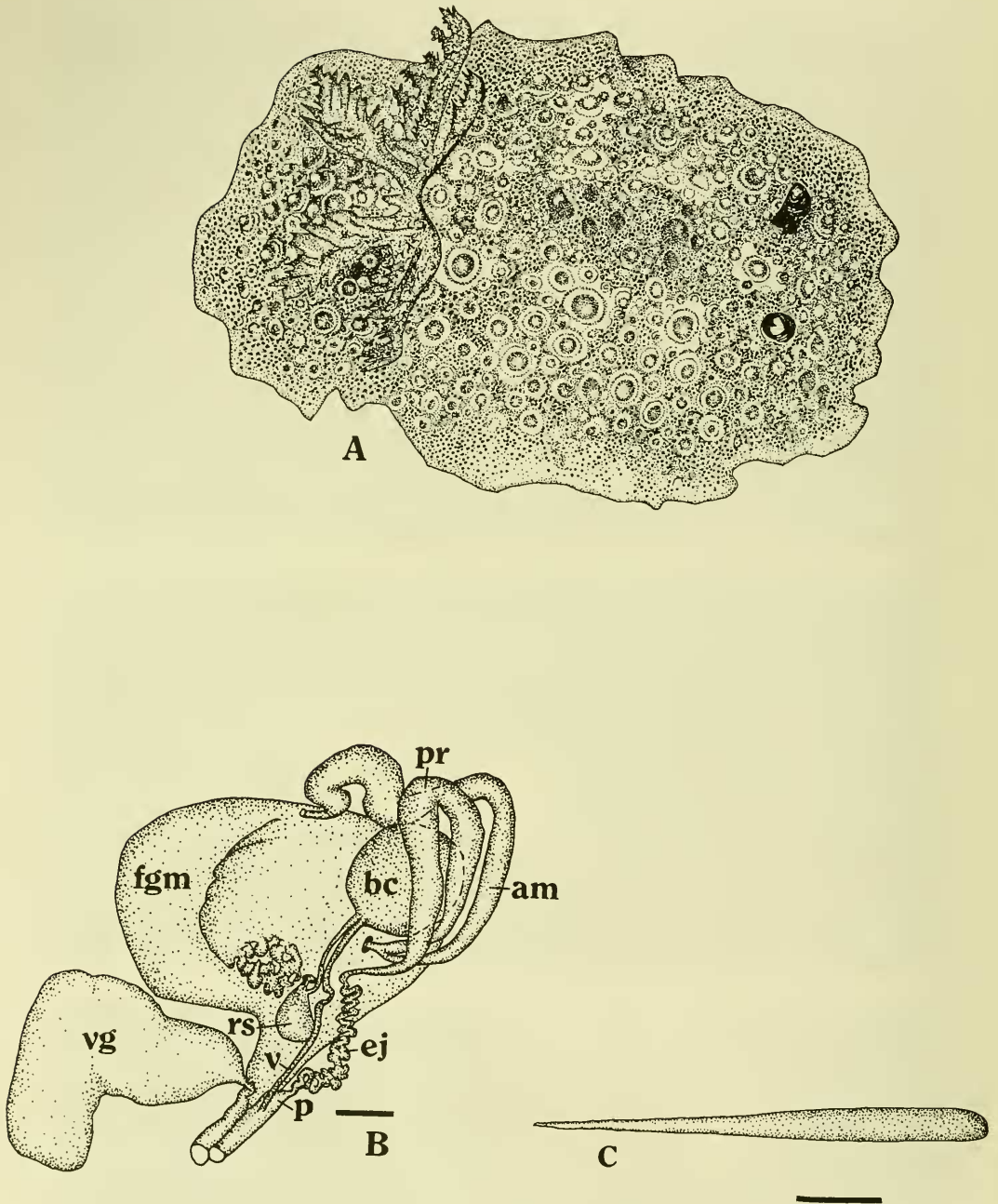


FIGURE 2. *Hoplodoris estrelgado* sp. nov. A. Living animal. B. Reproductive system, am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vg = vestibular gland, scale = 1.0 mm. C. Vestibular gland stylet, scale = 160 μ m.

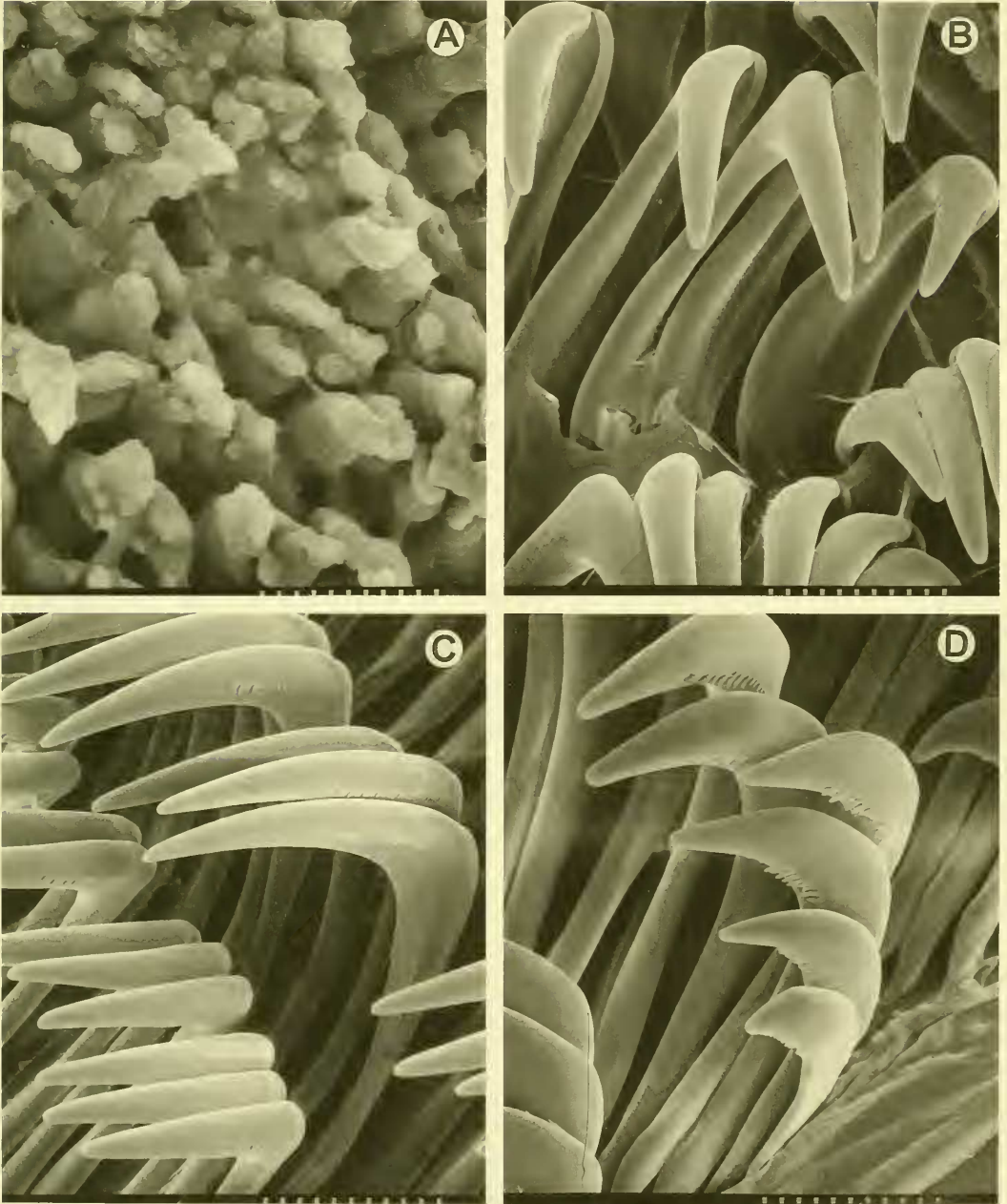


FIGURE 3. *Hoplodoris estrelyado* sp. nov. Scanning electron micrographs of buccal armature. A. Jaw rodlets, scale = 15 μ m. B. Inner lateral teeth, scale = 43 μ m. C. Lateral teeth from middle of the half-row, scale = 60 μ m. D. Outer lateral teeth, scale = 43 μ m.

cating into the oviduct and vas deferens. The short oviduct enters the female gland mass near the albumen gland. The thick proximal prostatic portion of the vas deferens is folded over itself once before it narrows into the long, narrow, highly convoluted, ejaculatory portion. The ejaculatory portion enters the short, wider penial bulb. The penis, which is adjacent to the slender vaginal duct at the common gonopore, is devoid of any armature, when stained and cleared. The female gland mass consists of the large mucous and membrane glands and a smaller albumen gland. The vagina is relatively long and straight with one partial loop. The proximal end of the vagina enters the large, spherical bursa copulatrix. Adjacent to the junction of the vagina and bursa is the thin duct which joins the thick-walled, club-shaped receptaculum seminis. This duct parallels the vagina for most of its length. The extremely short uterine duct also emerges from the receptaculum seminis and enters the female gland mass near the albumen gland. Near the exit of the mucous gland is a single, very large irregularly-shaped vestibular gland. The vestibular duct has an opening separate from the gonopore. The vestibular gland is armed with a long tapering stylet (Fig. 2C), which is visible when the distal end of the gland is stained and cleared. The stylet is 800 μm in length and is rounded at its proximal end. The stylet is not calcareous, as it was not dissolved when fixed in Bouin's fixative.

DISCUSSION. — The genus *Hoplodoris* was described by Bergh (1880) with *H. desmoparypha* designated as type species, by monotypy. The anatomy of this species has not been completely described, although several aspects of its morphology have been depicted by Bergh (1880, 1905). The external morphology and color of the living animals were not described. The characters that Bergh (1905) used to distinguish the genus were: presence of jaw rodlets, penial spines and a vestibular gland with a hollow, cornicopiate spine. Burn (1969) considered *Doris nodulosa* Angas, 1864 as a species of *Hoplodoris*, based on the facts that it has penial spines and a vestibular gland with an armed stylet. Thompson (1975) confirmed the presence of a vestibular gland and penial spines, although neither author illustrated the reproductive structures of this species. Miller (1991) redescribed the anatomy of *Homidoris novaecelandiae*

Bergh, 1904 and transferred this species to *Hoplodoris* on the basis that it has two distinct vestibular glands with hollow, conical stylets and a series of penial spines. These are the only three nominal species definitely placed in *Hoplodoris*.

Thompson (1975), following his description of Australian specimens of *Hoplodoris nodulosa*, considered *Carminodoris* Bergh, 1889 as a junior synonym of *Hoplodoris*, stating that *Carminodoris* appears to be unnecessary since almost all of its characters can be embraced by the older *Hoplodoris*. Thompson noted that there were anatomical differences between the specimens of *H. nodulosa* he examined and those described by Kay and Young (1969) as *Carminodoris nodulosa*. He attributed these differences to the fact that Kay and Young did not serial section their material. However, there are other anatomical differences between the Hawaiian and Australian material, such as the denticulation of the radular teeth, that suggest that they are not conspecific. It is likely that Thompson's material is conspecific with Angas' *Doris nodulosa* since it is collected near the type locality, near Sydney, New South Wales. Kay and Young's material probably represents an undescribed species. Absence of a stylet in the vestibular gland must be confirmed in the Hawaiian material.

When the anatomy of the described species placed in *Carminodoris* and *Hoplodoris* is compared (Table 1), considerable variation between species is evident. All species have a nodular dorsal surface with numerous rounded tubercles. The radular teeth may be smooth or denticulate (Baba 1993). The penis and vagina may be lined with spines or may be unarmed. One or more vestibular glands may be present, which may be large or small, sessile or at the end of an elongate duct. The glands may be unarmed, armed with a curved, hollow spine or a solid, straight stylet. These differences are not correlated with each other and each species possesses a unique combination of characters. This suggests that Thompson's synonymy of *Carminodoris* with *Hoplodoris* may be justified and is here provisionally maintained.

Hoplodoris estreyado differs from all other described species of *Hoplodoris* and *Carminodoris* in several regards. It is the only species in which all the teeth are denticulate. Only *H. grandiflora* (Pease, 1860) and *H. estreyado* have an unarmed penis (Kay and Young 1969; present

TABLE 1. Morphological variation in *Hoplodoris* and *Carmunodoris* species.

Species	Radular teeth	Vas deferens	Penis	Vagina	Vestibular glands			Armature
					Number	Position	Shape	
<i>C. armata</i>	all smooth	slightly convoluted	armed	unarmed	1	sessile	club	absent
<i>C. bifurcata</i>	middle teeth smooth	slightly convoluted	armed	unarmed	0 (?)	absent	absent	absent
<i>C. grandiflora</i>	inner smooth	highly convoluted	armed	armed	1	on elongate duct	sausage	absent
<i>C. mauritiana</i>	inner smooth	?	armed	?	?	?	?	?
<i>C. "nodulosa"</i> Hawaii	inner & outer smooth	highly convoluted	unarmed	unarmed	1	on elongate duct	sausage	absent
<i>H. desmoparypha</i>	all smooth	short	armed	unarmed	1	on elongate duct	spherical	unarmed
<i>H. estrellyado</i>	none smooth	highly convoluted	unarmed	unarmed	1	on elongate duct	spherical	unarmed
<i>H. nodulosa</i> Australia	inner & middle smooth	?	armed	unarmed	1	?	?	stylet
<i>H. novaezealandiae</i>	all smooth	slightly convoluted	armed	unarmed	2	sessile	club	hollow spine

study). *Hoplodoris estrelyado* and *H. desmoparypha* are the only two species that have a large spherical vestibular gland that is situated at the end of an elongate duct. It appears that *H. estrelyado* and Australian specimens of *H. nodulosa* are unique in having an elongate, solid stylet associated with the vestibular gland.

Confirmation of the generic placement of *H. estrelyado* must await further study of other members of the genus. *Hoplodoris desmoparypha*, the type species of the genus, has not been recorded since its original and subsequent descriptions by Bergh (1880, 1905) and nothing is known about the color of the living animals. Similarly, the type species of *Carminodoris*, *C. mauritiana*, is known only from the original description (Bergh 1889) and its anatomy and the morphology of the living animal remain unknown. The absence of vestibular gland stylets in Hawaiian specimens identified as *C. nodulosa* and *C. grandiflora* require confirmation. Following the accumulation of this anatomical data, construction of a phylogenetic hypothesis testing the monophyly of these taxa must be undertaken.

Members of other dorid genera (including *Asteronotus* Ehrenberg, 1831, *Sclerodoris* Eliot, 1903, *Jorunna* Bergh, 1876 and *Kentrodoris* Bergh, 1876) possess a vestibular gland. In *Asteronotus* the notum is ornamented with large, irregularly angled tubercles arranged in ridges rather than having densely arranged, rounded tubercles as in *Hoplodoris* (including *Carminodoris*). Also, jaw rodlets are absent in *Asteronotus* but are present in members of the latter genus. Species of *Sclerodoris*, *Jorunna* and *Kentrodoris* have the notum ornamented with spiculate caryopyllidia rather than rounded tubercles and lack jaw rodlets. In *Sclerodoris* the vestibular gland is sessile and lacks any armature while in *Jorunna* and *Kentrodoris* the gland has a long duct and a stylet as in *Hoplodoris*. Detailed comparisons of this taxa with *Hoplodoris* must await a comprehensive parsimony-based phylogenetic study of the cryptobranch dorids to ascertain which similarities are due to common ancestry and which represent independent acquisition of these characters.

Taringa luteola (Kelaart, 1858)
(Figs. 1B, 4, 5)

Doris luteola Kelaart, 1858:103.

Thordisa caudata Farran, 1905:340, pl. 2, figs. 18, 19.

Trippa luteola (Kelaart) Eliot, 1906:658, pl. 42, fig. 4.

MATERIAL EXAMINED. — CASIZ 099361, one specimen, dissected, 1 m depth, Manuhuanja Island, Mtwara Region, Tanzania, 1 November 1994, T. M. Gosliner. CASIZ 099231, one specimen, 1 m depth, Manuhuanja Island, Mtwara Region, Tanzania, 2 November 1994, T. M. Gosliner.

DISTRIBUTION. — Thus far, this species is known only from the western Indian Ocean of Madagascar (Eliot 1906), Tanzania (present study) and Sri Lanka (Kelaart 1858; Farran 1905).

EXTERNAL MORPHOLOGY. — Preserved animals are 15–22 mm in length. The living animals (Fig. 1B) are cream white with low, pointed tubercles. There is a yellow band along the entire margin of the mantle. An additional interrupted ring of yellow pigment is found in the central portion of the mantle extending from just posterior to the rhinophores to the region immediately anterior to the gills. The gills are white with brown to gray marginal pigment around the ultimate branches of the gill. The rhinophores are dark gray to black. The tubercles have a few irregular, digitate papillae extending from their dorsal surface (Fig. 4A). On either side of the head is a long, digitiform tentacle. The anterior end of the foot is bilabiate. The branchial plume, composed of six sparsely branched, bi- to tripinnate gill branches, is large, nearly as wide as the body. A black line extends up the edge of each gill branch. The perfoliate rhinophores bear about 16 lamellae.

BUCCAL ARMATURE. — The buccal mass is large and muscular, with elongate curved salivary glands. At the anterior end of the muscular portion of the buccal mass is the thin chitinous labial cutical. It contains some thicker regions but is entirely devoid of chitinous rodlets. The radular formula is $28 \times 37\text{--}39.1.37\text{--}39$ in one specimen examined. The rachis (Fig. 5A) contains a row of thin, elongate rachidian plates. The inner lateral teeth are simply hamate and curved with two triangular denticles. The first 30 teeth (Fig. 5B) have 1–2 denticles while the next 1–3 teeth lack any trace of a denticle. The outer 3–4

teeth (Fig. 5C) are much shorter and have a finely fimbriate margin of elongate, bristly spines.

REPRODUCTIVE SYSTEM. — The reproductive system is triaulic (Fig. 4B). The ampulla is thick, elongate and tubular, narrowing somewhat before bifurcating into an oviduct and vas deferens. The short oviduct enters the female gland mass near the albumen gland. The proximal prostatic portion of the vas deferens is not much wider than the ejaculatory portion and is folded over itself once before it narrows slightly into the long, muscular ejaculatory portion. The ejaculatory portion consists of several loops. It narrows and then enters the moderately long penial bulb, which is devoid of armature but contains a thin cuticular lining near its apex (Fig. 4C). The penis is adjacent to the narrower vaginal duct at the common gonopore. The female gland mass consists of the large mucous gland and smaller membrane and albumen glands. The vagina is relatively long and curved. The proximal end of the vagina enters the base of the thin walled,

spherical bursa copulatrix. Adjacent to this is a somewhat shorter thin duct to the pyriform receptaculum seminis. The short uterine duct emerges from the base of the receptaculum and enters the female gland mass near the albumen gland. This species lacks any genital armature.

DISCUSSION. — *Doris luteola* was originally described from Sri Lanka (Kelaart, 1858). Eliot (1906) described aspects of the anatomy of specimens from the eastern coast of Madagascar. Eliot considered *Thordisa caudata* Farran, 1905 as a junior synonym of *Doris luteola*, based on their similar color patterns and presence in Sri Lanka. Eliot transferred this species from *Doris* and *Thordisa* to *Trippa* on the basis that it has compound tubercles and pylaine glands present on the buccal mass in addition to salivary glands. He also redescribed *Trippa ornata* Bergh 1880, type species of the genus *Trippa*, and strongly suggested that it is a synonym of *Doris intecta* Kelaart, 1859. Edmunds (1971) considered *T. ornata* as a junior synonym of *Trippa intecta* and

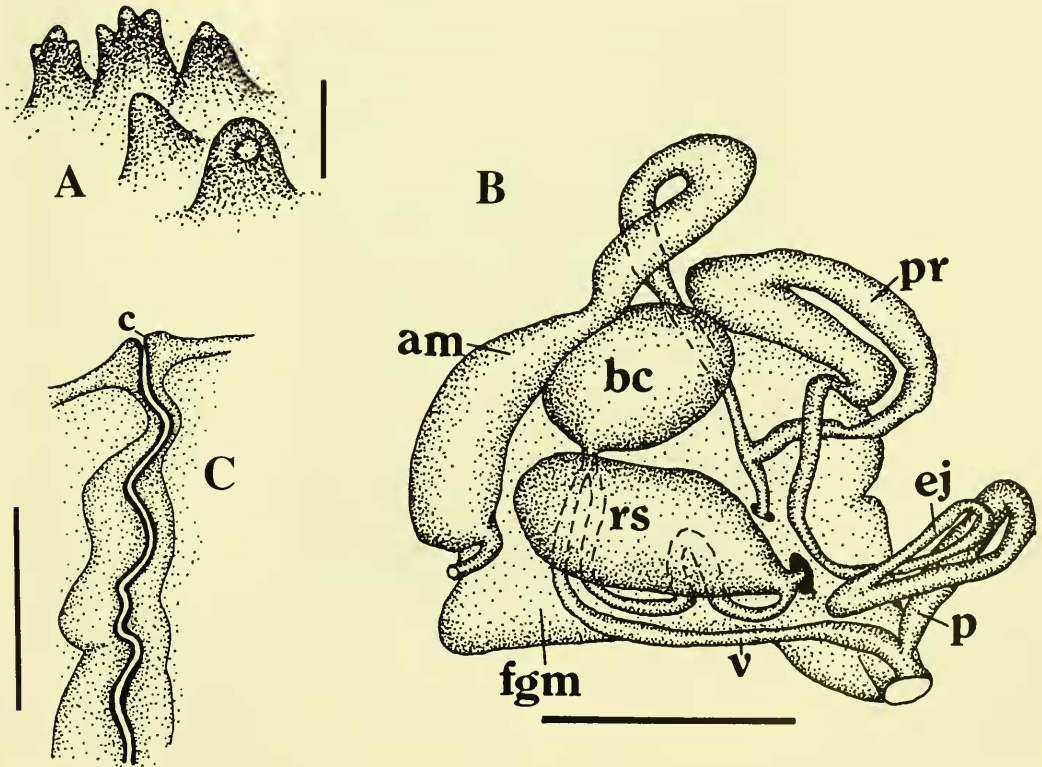


FIGURE 4. *Taringa luteola* (Kelaart, 1858). A. Detail of tubercles, scale = 1.0 mm. B. Reproductive system, am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, scale = 1.0 mm. C. Cuticular lining of vas deferens, c = cuticle, scale = 70 μ m.

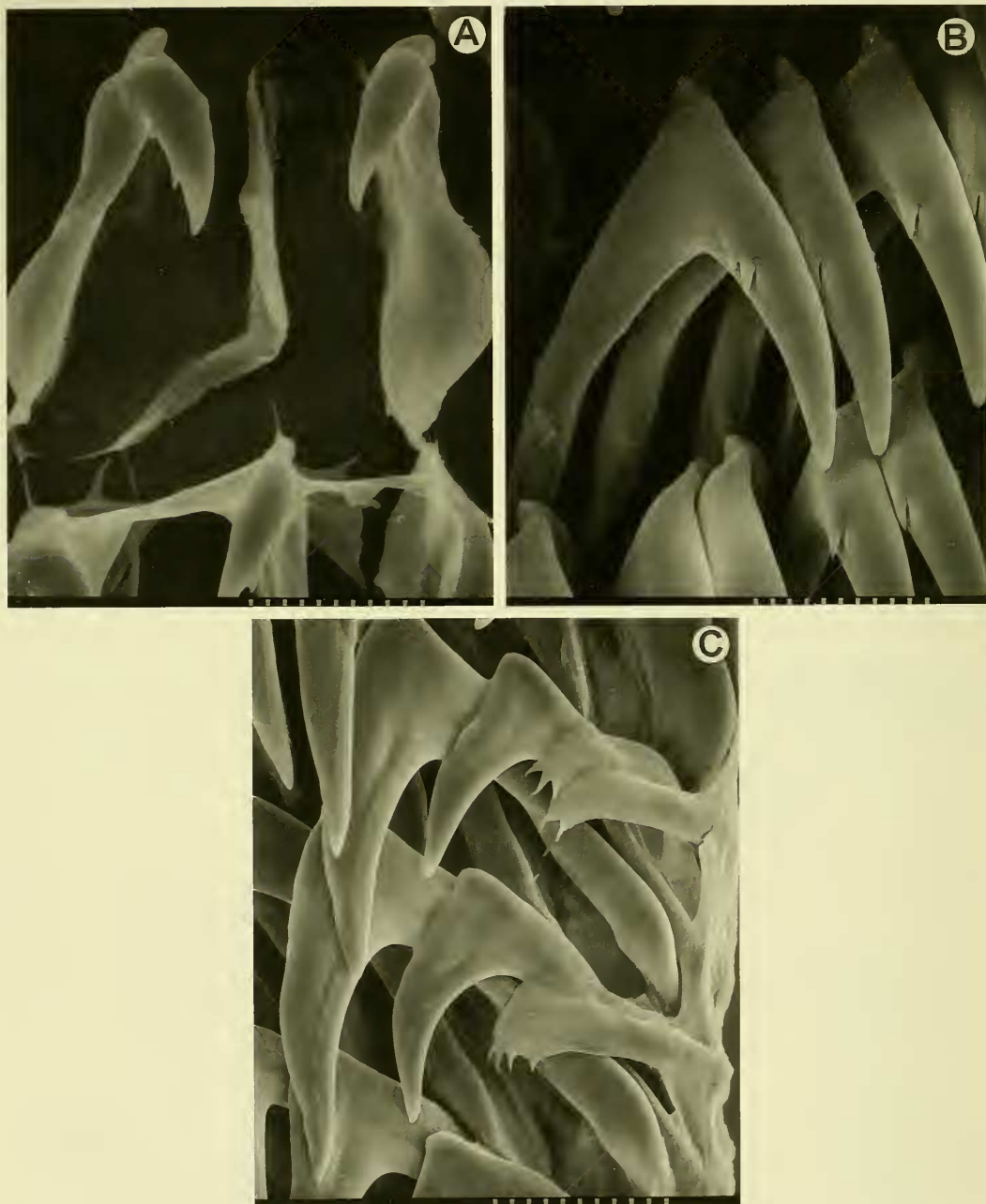


FIGURE 5. *Taringa lueola* (Kelaart, 1858). Scanning electron micrographs of radula. A. Rachidian and inner lateral teeth, scale = 20 μm . B. Lateral teeth from middle of the half-row, scale = 30 μm . C. Outer lateral teeth, scale = 43 μm .

described its anatomy in greater detail. We confirmed this synonymy by re-examining the holotype of *T. ornata* in the Zoologisk Museum, University of Copenhagen. This species differs from *Taringa luteola* in several important regards. The buccal mass of *Trippa intacta* has a small glandular portion (Edmunds 1971, fig. 8d) anterior to the insertion of the lateral musculature. Such glands were not found in *Taringa luteola*. All of the radular teeth of *Trippa intacta* are simply hamate and devoid of auxillary denticles or bristles. The radula of *Taringa luteola* has a row of vestigial rachidian teeth that are absent in *Trippa intacta*. Most of the lateral teeth have a single small denticle and the outer three laterals have fine, elongate bristles along their margin. The vaginal duct of *Taringa luteola* is far more elongate than that of *Trippa intacta*.

Three other genera of dorids have radular teeth that are similar to those of *Doris luteola*. Species of *Thordisa* Bergh, 1877, *Aporodoris* Ihering, 1886, and *Taringa* Marcus, 1955, all have elongate bristles on the outermost radular teeth. The latter two genera have denticles on most of the other lateral teeth, while denticles are absent in species of *Thordisa*. Marcus and Marcus (1967) stated that the two genera differ only by the presence of penial armature in *Taringa* and its absence in *Aporodoris*. Thompson and Brown (1981) considered *Aporodoris* as a junior synonym of *Discodoris*, based on a re-examination of the type material of *Doris millegrana* Alder and Hancock, 1854, type species of *Aporodoris*. Thompson and Brown united the genera despite the fact that most species of *Discodoris*, including the type species, *Discodoris boholiensis* Bergh, 1877, lack denticles on the radular teeth. It appears that *Aporodoris* is more similar to *Taringa* than to *Discodoris*, but confirmation of its systematic placement requires detailed anatomical study of the penial papilla and subsequent phylogenetic analysis. The present species bears considerable resemblance to species of *Taringa*, in that the majority of radular teeth have denticles and the distal portion of the vas deferens has a cuticular lining. The absence of a distinctly thickened cuticular ring and the presence of a vestigial row of rachidian teeth distinguishes *Doris luteola* from other described members of *Taringa*.

***Taringa halgerda* sp. nov.**

(Figs. 1C, 6, 7)

Cadlinella sp. Debelius, 1996:217, top photo.

TYPE MATERIAL. — Holotype: CASIZ 106469, one specimen, Bus Stop Reef, Balayan Bay, Batangas Province, Luzon, Philippine Islands, 13 m depth, 18 April 1996, T. M. Gosliner. Paratypes: CASIZ 110427, five specimens (one dissected), Bus Stop Reef, Balayan Bay, Batangas Province, Luzon, Philippine Islands, 3 m depth, 23 April 1997, D. W. Behrens. CASIZ 083731, two specimens, Bus Stop Reef, Balayan Bay, Batangas Province, Luzon, Philippine Islands, 3 m depth, 21 February 1992, M. D. Miller.

ETYMOLOGY. — The trivial name *halgerda* was chosen to indicate the overall, external, morphological similarity between this species and members of the genus *Halgerda*.

DISTRIBUTION. — Thus far, this species is known only from the Philippine Islands (present study), from a photograph by Takamasa Tonozuka from Bali, Indonesia (Debelius 1996) and from a photograph by Jim Black from Milne Bay, Papua New Guinea.

NATURAL HISTORY. — *Taringa halgerda* is found on the outer edges of rock walls and reef fronts in shallow water. The egg mass is a densely packed, open coiled ribbon, attached to the substrate along its edge. It has a characteristic pale blue color and is about 20 mm in diameter.

EXTERNAL MORPHOLOGY. — Preserved animals are 22–33 mm in length. The living animals (Fig. 1C) are white with low, flat, yellow tubercles (Fig. 6A). The tubercles are digitate, with short, round papillae extending from their posterior surface (Fig. 6B). The largest are capitate with a narrow, short base. These are found medially on the dorsum. The anterior end of the foot is bilabiate and notched. On either side of the head is a long, digitiform tentacle. The branchial plume, comprised of six sparsely branched, multipinnate gill branches, is large, nearly twice the width of the body in diameter. The anus is situated within the circle formed by the gill branches. The size and shape of the gill represent the basis for considering this species “*Halgerda*-like” in its appearance. A black line extends up the edge of each gill branch. The black, perfoliate rhinophores bear about 17–18 lamellae.

BUCCAL ARMATURE. — The buccal mass is large and muscular. At the anterior end of the

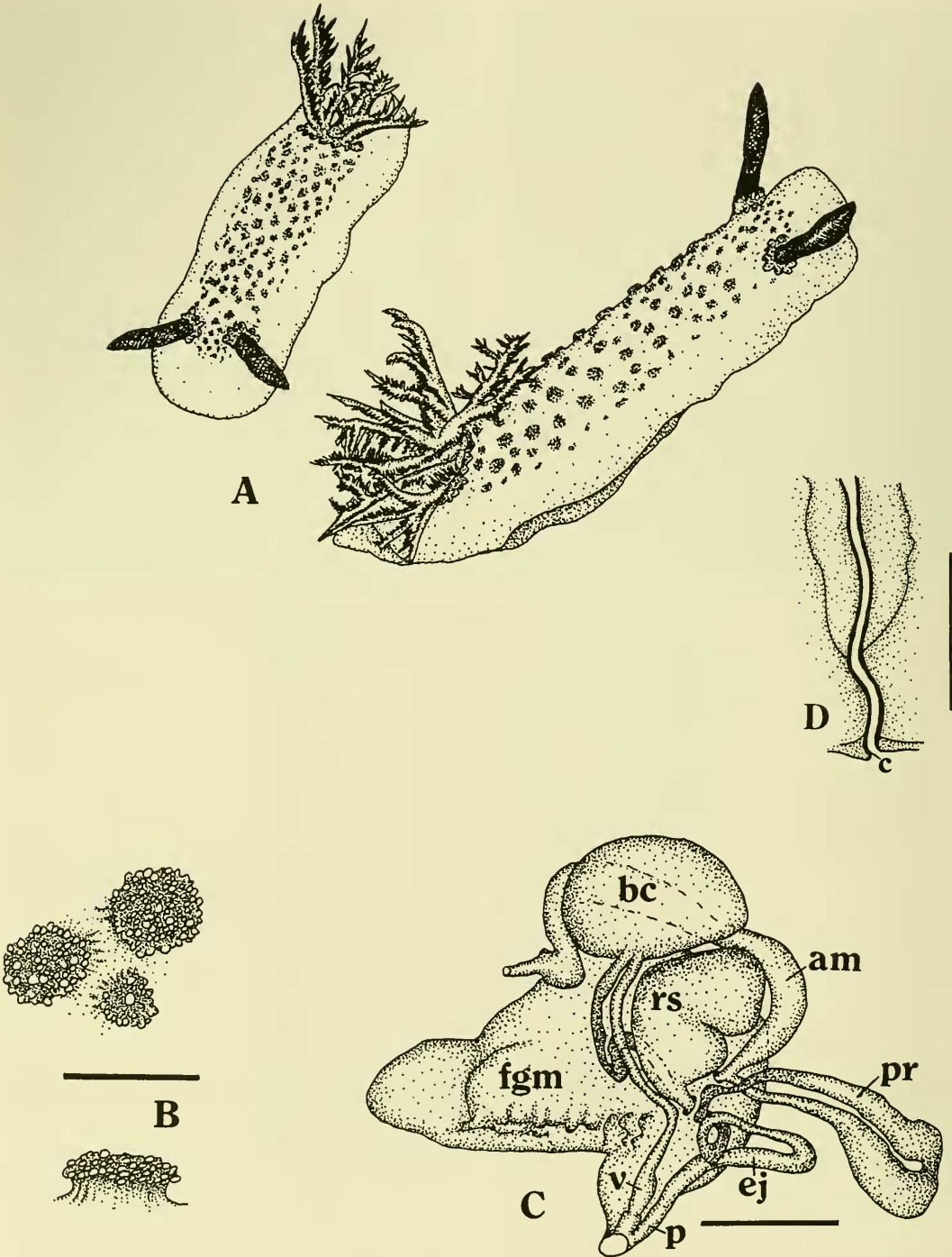


FIGURE 6. *Taringa halgerda* sp. nov. A. Living animals. B. Detail of tubercles, scale = 1.0 mm. C. Reproductive system, am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, scale = 1.0 mm. D. Cuticular lining of vas deferens, c = cuticle, scale = 70 μ m.

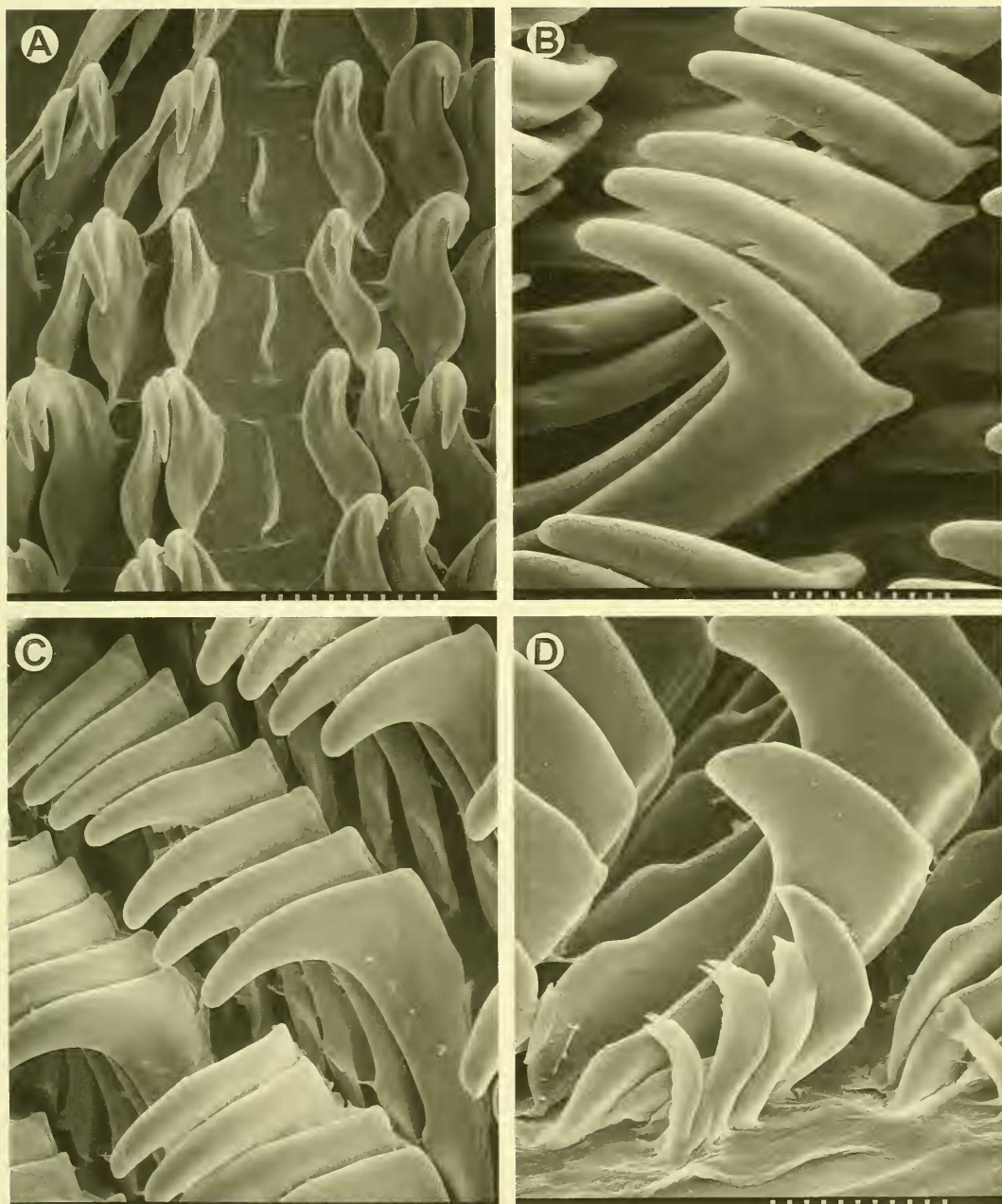


FIGURE 7. *Taringa halgerda* sp. nov. Scanning electron micrographs of radula. A. Rachidian and inner teeth, scale = 60 μ m. B. Lateral teeth from middle of the half-row, scale = 25 μ m. C. Lateral teeth devoid of denticles, scale = 60 μ m. D. Outer lateral teeth, scale = 43 μ m.

muscular portion of the buccal mass is the thin chitinous labial cutical. It contains some thicker regions but is entirely devoid of chitinous rodlets. The radular formula is $33 \times 40.1.40$ in one specimen examined. The rachis (Fig. 7A) contains a row of thin, elongate rachidian plates. The inner lateral teeth are simply hamate and curved with a single triangular denticle. The first 30 teeth (Fig. 7B) have a single denticle while the next 5–10 teeth lack any trace of a denticle. The outer 3 teeth (Fig. 7C) are much shorter and have a finely fimbriate margin of elongate, bristly spines.

REPRODUCTIVE SYSTEM. — The reproductive system is triaulic (Fig. 6C). The ampulla is thick, elongate and tubular, narrowing somewhat before bifurcating into an oviduct and vas deferens. The short oviduct enters the female gland mass near the albumen gland. The proximal prostatic portion of the vas deferens is not much wider than the ejaculatory portion and is folded over itself once before it narrows slightly into the long, muscular, ejaculatory portion. The ejaculatory portion is relatively short and contains one short loop. It narrows and then enters the short penial bulb, which is devoid of armature, but contains a thin cuticular lining near its apex (Fig. 6D). The penis is adjacent to the narrower vaginal duct at the common gonopore. The female gland mass consists of the large mucous gland and smaller membrane and albumen glands. The unarmed vagina is relatively long and curved. The proximal end of the vagina enters the base of the thin walled, spherical bursa copulatrix. Adjacent to this is an equally long, thin duct which joins the bursa to the kidney-shaped receptaculum seminis. The short uterine duct emerges near this junction and enters the female gland mass near the albumen gland. This species lacks any genital armature.

DISCUSSION. — *Taringa halgerda* is similar to *T. luteola* in most aspects of its anatomy. Both species have a similar color pattern, compound tubercles, a radula with a vestigial row of rachidian teeth, denticulate teeth and a simple, triaulic reproductive system. However, the two species differ in several regards. *Taringa halgerda* lacks the yellow marginal line and the incomplete interior yellow ring on the center of the mantle that are present in *T. luteola*. Rather, *T. halgerda* has yellow pigment restricted to the surface of the large tubercles in the central por-

tion of the notum. The tubercles of *T. halgerda* are larger, more rounded and have more papillae extending from their apices than do those of *T. luteola*. The largest tubercles of *T. halgerda* are capitate while those of *T. luteola* are all conical. The gills of *T. halgerda* are proportionately larger than those of *T. luteola*.

The radular teeth of *T. halgerda* have blunter cusps than do those of *T. luteola*. The teeth of *T. luteola* may have either one or two denticles while in *T. halgerda* the teeth have only a single denticle. More of the outer teeth lack denticles in *T. halgerda* than in *T. luteola*.

The reproductive system of *T. halgerda* is similar in its morphology to that found in *T. luteola*. The primary difference between the two species is that the ejaculatory portion of the vas deferens is slightly more elongate and convoluted in *T. luteola*.

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LITERATURE CITED

- BABA, K. 1993. Two new species of *Carminodoris* (Nudibranchia: Dorididae) from Japan. *Venus* 52(3):223–234.
- BERGH, R. 1880. Malacologische Untersuchungen, 4. *In* Reisen im Archipel der Philippinen. Zweiter Theil. Wissenschaftliche Resultate Suppl. 2, 1:1–78, C. Semper, ed. Leipzig.
- . 1889. Malacologische Untersuchungen, 3. *In* Reisen im Archipel der Philippinen. Zweiter Theil.

- Wissenschaftliche Resultate 16(2):815–872, C. Semper, ed. Leipzig.
- . 1905. Malacologische Untersuchungen, 6. *In* Reisen im Archipel der Philippinen. Zweiter Theil. Wissenschaftliche Resultate 9:57–115, C. Semper, ed. Leipzig.
- BURN, R. 1969. A memorial report on the Tom Crawford Collection of Victorian Opisthobranchia. *Journal of the Malacological Society of Australia* 12:64–106.
- DEBELIUS, H. 1996. Nudibranchs and sea snails. Indo-Pacific field guide. IKAN—Unterwasserarchiv, Frankfurt. 321 pp.
- EDMUNDS, M. 1971. Opisthobranchiate Mollusca from Tanzania (Suborder: Doridacea). *Zoological Journal of the Linnean Society* 50(4):339–396.
- ELIOT, C. 1906. On the nudibranchs of southern India and Ceylon, with special reference to the drawings by Kelaart and the collections belonging to Alder and Hancock preserved in the Hancock Museum at Newcastle-on-Tyne. *Proceedings of the Zoological Society of London for 1906*:636–691.
- FARRAN, G. P. 1905. Report on the opisthobranchiate Mollusca collected by Professor Herdman, at Ceylon, in 1902. Pp. 329–364 *in* Report to the government of Ceylon on the pearl oyster fisheries of the Gulf of Manaar 3, Suppl. Rept. No. 21, W. A. Herdman, ed. Royal Society, London.
- GHISELIN, M. T. 1992. How well known is the opisthobranch fauna of Madang, Papua New Guinea? *Proceedings of the Seventh International Coral Reef Symposium* 2:697–701.
- GOSLINER, T. M. 1992. Biodiversity of tropical opisthobranch gastropod faunas. *Proceedings of the Seventh International Coral Reef Symposium* 2:702–709.
- GOSLINER, T. M. AND D. W. BEHRENS. 1997. Description of four new species of phanerobranch dorids (Mollusca: Nudibranchia) from the Indo-Pacific, with a redescription of *Gymnodoris aurita* (Gould, 1852). *Proceedings of the California Academy of Sciences* 49(9):287–308.
- . 1998. Five new species of *Chromodoris* (Mollusca: Nudibranchia: Chromodorididae) from the tropical Indo-Pacific Ocean. *Proceedings of the California Academy of Sciences* 50(5):139–165.
- GOSLINER, T. M., D. W. BEHRENS, AND G. C. WILLIAMS. 1996. Coral reef animals of the Indo-Pacific. Sea Challengers, Monterey, California. 314 pp.
- GOSLINER, T. M. AND R. DRAHEIM. 1996. Indo-Pacific opisthobranch gastropod biogeography: how do we know what we don't know? *American Malacological Bulletin* 12(1/2):37–43.
- KAY, E. A. AND D. K. YOUNG. 1969. The Doridacea (Opisthobranchia: Mollusca) of the Hawaiian Islands. *Pacific Science* 23(2):172–231.
- KELAART, E. F. 1858. Description of new and little known species of Ceylon nudibranchiate molluscs and zoophytes. *Journal of the Royal Asiatic Society, Ceylon Branch, Colombo* 3(1):84–139.
- MARCUS, EV. AND ER. MARCUS. 1967. Tropical American opisthobranchs. *Studies in Tropical Oceanography Miami* 6:3–137.
- MILLER, M. C. 1991. On the identity of the dorid nudibranch *Homoiodoris novaezealandiae* Bergh, 1904 (Gastropoda: Opisthobranchia). *Journal of Natural History* 25:293–304.
- THOMPSON, T. E. 1975. Dorid nudibranchs from eastern Australia (Gastropoda, Opisthobranchia). *Journal of the Zoological Society of London* 176:177–517.
- THOMPSON, T. E. AND G. H. BROWN. 1981. Allocation of the nudibranch *Doris millegrana* Alder and Hancock, 1854 to the genus *Discodoris* Bergh, 1877, after re-examination of the type material. *Zoological Journal of the Linnean Society* 72(3):263–266.